NONLINEARITIES, SCALE-DEPENDENCE, AND INDIVIDUALISM OF BOREAL FOREST TREES TO CLIMATE FORCING

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INTRODUCTION

- Changes in climate are affecting tree growth, fire regimes and the geographic ranges of species (Beck *et al.* 2011; Kelly *et al.* 2013)
- Increasing our understanding of how boreal tree species respond to climate warming is critical for predicting the future states of the boreal forest and assessing the global impacts of these changes
- Black spruce (*Picea mariana* [Mill.] B.S.P.) is the most abundant tree species in the Interior Alaskan boreal forest
- Although it grows in a variety of community types (Hollingsworth *et al.* 2006), it is the only tree species found at the coldest, wettest sites on the landscape
- Despite its abundance, very little is known about the climate-growth relationships of black spruce, as the majority of dendrochronological studies in Interior Alaska involve white spruce growth divergence

Growth Divergence in Boreal Conifers

- Trees in the circumboreal forest have become less sensitive to temperature throughout the 20th century
  - This decoupling of growth from temperature has been termed the "divergence problem" (D'Arrigo *et al.* 2008)
- Individual trees may also exhibit varying and even opposing responses to the same climate drivers (Wilmking *et al.* 2005), a phenomenon referred to as "divergent growth"
  - We use the term "*inter-tree growth divergence*" to refer to these inter-tree differences in growth
- Although well documented in white spruce (Wilmking *et al.* 2004, 2005), it is unclear how widespread *inter-tree growth divergence* is among black spruce

STUDY OBJECTIVES

- **Overall goal:** Assess how widespread the phenomenon of *inter-tree growth divergence* is in black spruce in Alaska's boreal forest
- **Objectives:**
  i. Evaluate how *site-level* climate-growth relationships vary along an environmental gradient;
  ii. Determine if black spruce exhibits heterogeneous responses to climate by evaluating *tree-level* climate-growth relationships; and
  iii. Describe how the *site-* and *tree-level* climate-growth relationships of black spruce change over space and time

METHODS

Tree-Ring Samples

- Cores were collected from trees at the *Summit* (Fig. 1a), *Side slope*, *Toe slope* and *Valley bottom* (Fig. 1b) of a steep, north-facing toposequence located north of Fairbanks, Alaska

Figure 1. *Summit* (a) and *Valley bottom* (b) sites of steep, north-facing toposequence. Note that the architecture of the trees differs widely between the sites.

- The cores were mounted, sanded, measured and cross-dated
- Ring-width series were detrended to remove the geometric growth trend
- Both *site-level* and *tree-level* chronologies were developed

Analysis of Site-Level and Tree-Level Climate-Growth Relationships

- DENDROCLIM (Biondi &Waikul 2004) was used to evaluate the climate-growth relationships
- *Site-* and *tree-level* chronologies were correlated with mean monthly temperature (MMT) and total monthly precipitation (TMP) using a 12-month climate window (October of year *t-1* to September of year *t*) and a 50-year moving interval analysis
- We classified the univariate responses of the *site-* and *tree-level* chronologies to MMT and TMP into one of four response-types: positive (+), negative (-), mixed (m), or none (Lloyd *et al.* 2011)
- To evaluate the *site-level* multivariate growth responses to temperature (T) and precipitation (P), a count of the trees exhibiting each temperature-precipitation response-type combination (e.g., +Temperature and +Precipitation (+T+P)) was compiled for each site
- Response-type chronologies were then developed for each site by averaging the *tree-level* chronologies exhibiting the same response-type combination
- We then ran a 50-year moving interval analysis in DENDROCLIM on the dominant response-type chronologies for each site using the 12-month climate window described above

RESULTS

Site-Level Climate-Growth Relationships

- At the *site-level*, black spruce growth responses to temperature were generally negative or neutral
- Growth responses to precipitation were either positive or mixed (Fig. 2)

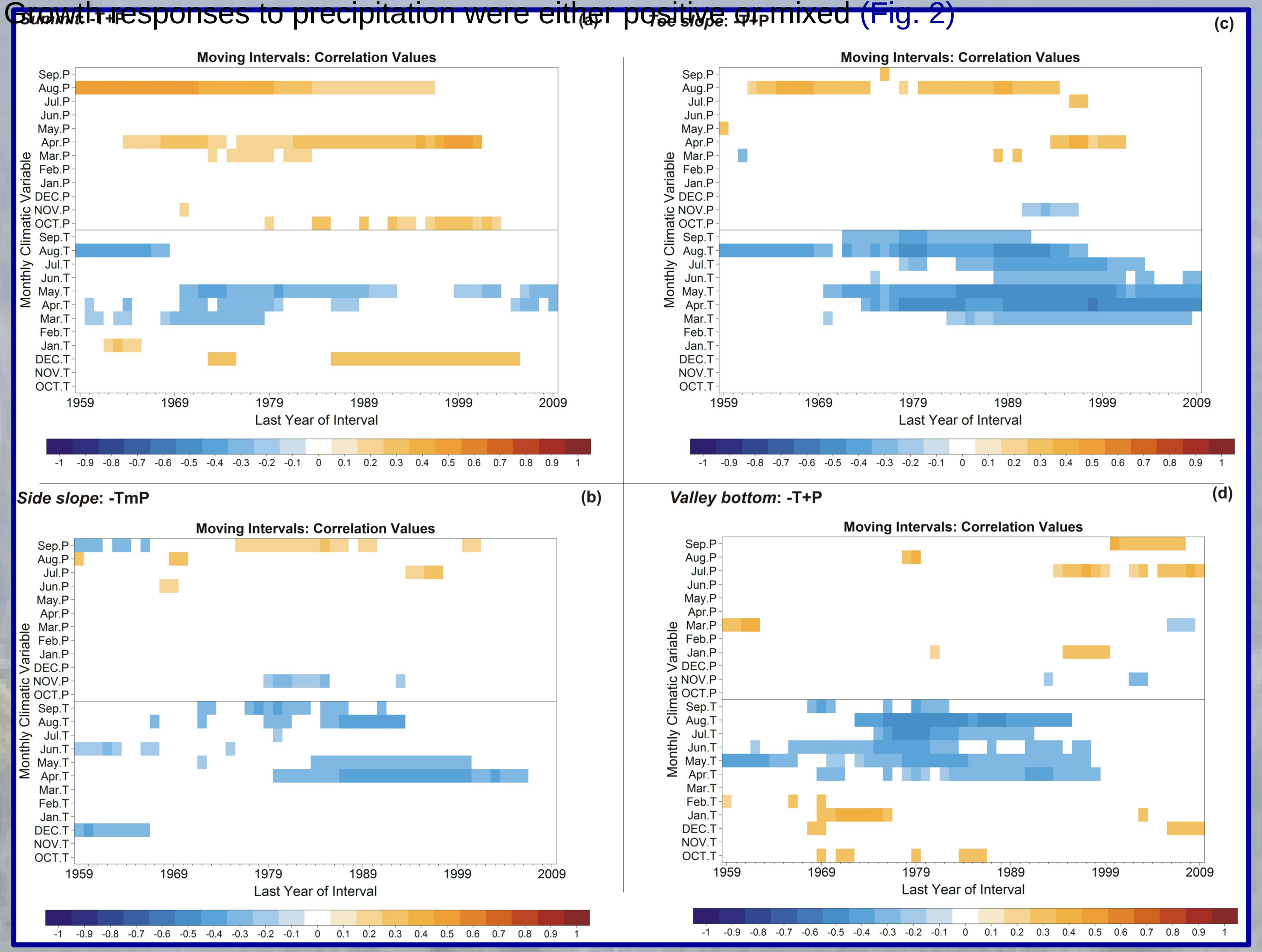
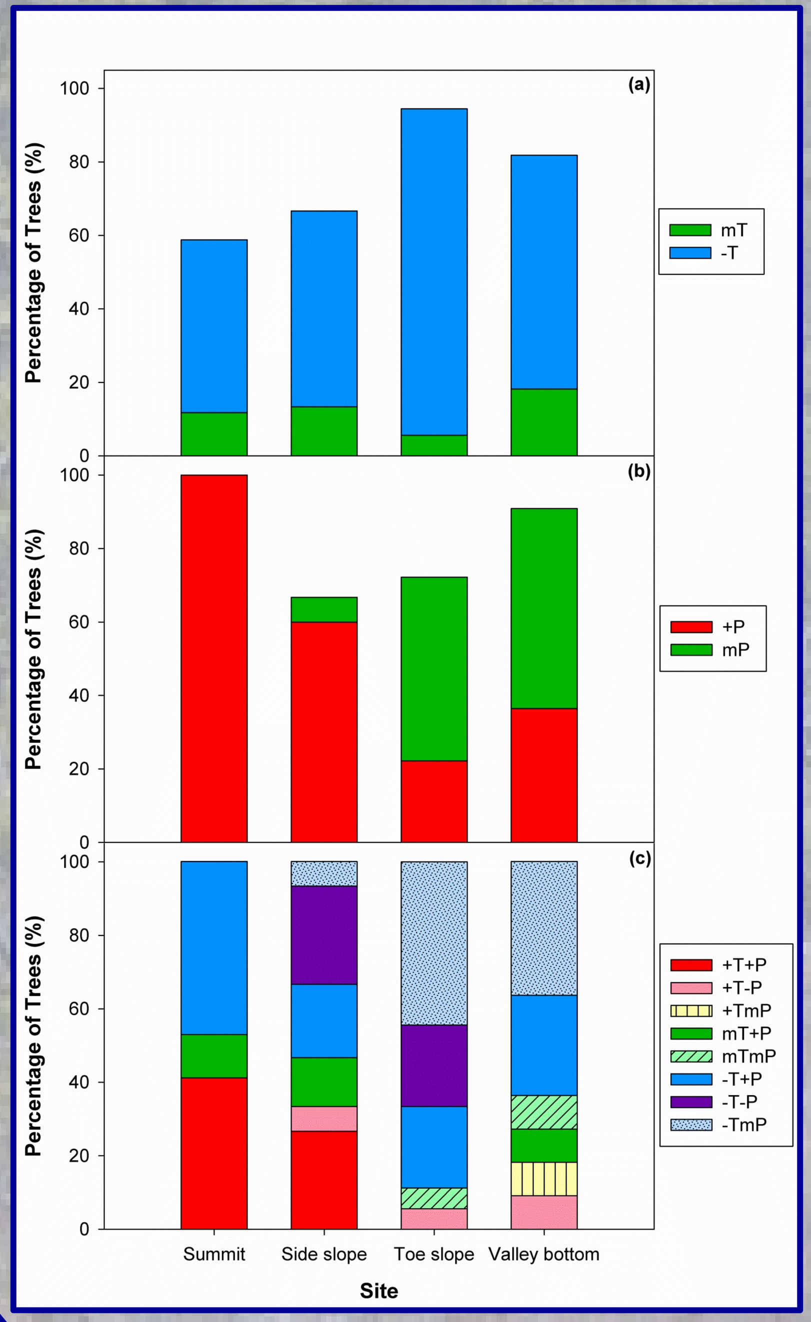


Figure 2. *Site-level* responses to warmer temperatures (T) and increased precipitation (P). Capitalized months (e.g., OCT) refer to previous year of growth and lowercase months (e.g., Oct) refer to current year of growth. Correlation values are the result of a 50-year moving interval analysis (see METHODS). Significant correlations are represented by blue shades for negative correlations and orange shades for positive ones. All non-significant correlations are set to 0.0 and appear white.

Tree-Level Climate-Growth Relationships



- Among individual trees, climate-growth relationships were not homogeneous both within- and between-sites
- The majority of trees responded negatively to warmer temperature (Fig. 3a) and positively to increased precipitation (Fig. 3b)
- Negative responses to warmer temperature generally increased downslope, while positive responses to precipitation increased upslope
- The *Valley bottom* had the greatest diversity of response-types (Fig. 3c)

Figure 3. Percentages of trees at each site exhibiting positive (+), negative (-) and mixed (m) responses to warmer temperatures (T) and increased precipitation (P). Trees were categorized by their univariate (e.g., +T refers to trees with a positive response to temperature) responses to temperature (a) and precipitation (b), and multivariate responses (c) to both temperature and precipitation based on the results of a 50-year moving interval analysis performed at the *tree-level*. Refer to METHODS for more details.

DISCUSSION

Site-level Responses to Climate

- At the *site-level* black spruce generally responds negatively to warmer temperatures and positively to increased precipitation during the growing season, regardless of topographic position (Fig. 2; Fig. 4)
- Differences in non-climatic factors associated with topographic position (Fig. 4) likely interact with climate to drive *site-level* growth responses in these trees
- Differences in tree architecture (Fig. 1) are associated with topographic position along this toposequence (Fig. 4), which may partially explain the variations in the growth patterns observed between-sites
- We speculate that **different mechanisms create drought stress in all slope positions**:
  1) At the *Summit*, drought stress occurs when evapotranspiration outstrips soil moisture during periods of low precipitation;
  2) At the *Valley bottom*, drought stress occurs via physiological limitations on water uptake in cold, wet and poorly aerated soils when air temperatures are unusually warm
- With continued warming, this moisture-mediated sensitivity to warm temperatures could inhibit black spruce reproduction and contribute yet another mechanism for the ecological regime shift predicted for the Interior Alaskan boreal forest (Kelly *et al.* 2013; Mann *et al.* 2012; Beck *et al.* 201

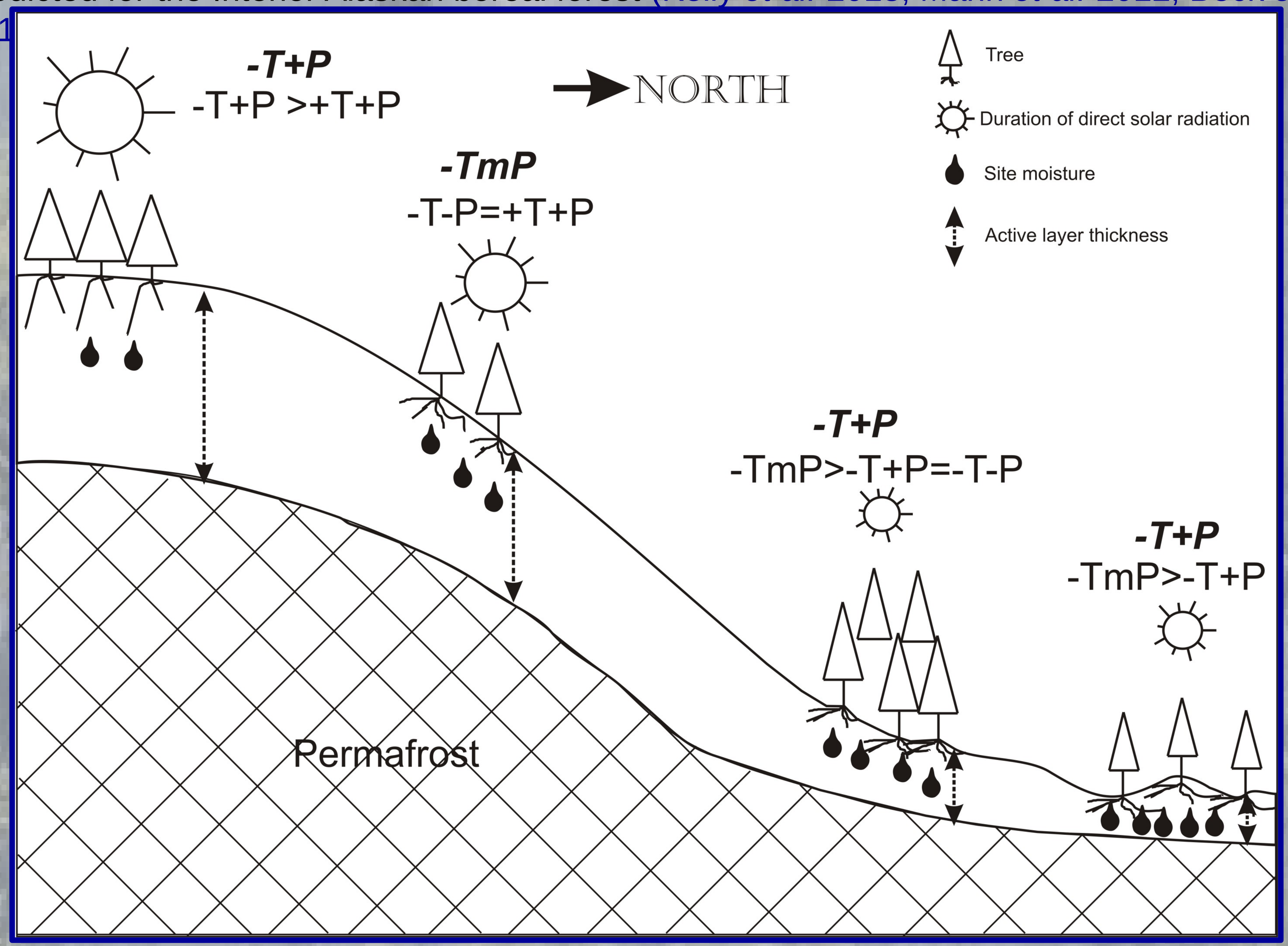


Figure 4. Schematic of north-facing toposequence illustrating the *site-level* (bold and italics) and dominant *tree-level* response-types observed, where '+', '-' and 'm' refer to positive, negative and mixed growth responses to temperature (T) and precipitation (P). Relative differences between sites are depicted for the density of trees, duration of direct solar radiation (size of symbol corresponds to the duration of direct solar radiation received throughout the 2011 snow-free season), site moisture (number of symbols corresponds to the amount of soil moisture), and active layer thickness.

Tree-Level Responses to Climate

- Response-type diversity increases downslope with increased microtopographic diversity, which Wilmking & Myers-Smith (2008) suggest is an important factor in determining inter-tree growth differences in black spruce's responses to climate
- *Inter-tree growth divergence* is common in black spruce, and is probably an inherent feature of black spruce's plastic growth strategy that enables this species to exist in some of the most extreme habitats for tree growth in the Subarctic
- The use of *site-* and *tree-level* climate-growth relationships provides complimentary perspectives on the complexity of the growth responses of black spruce to climate variability

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